Climatic shifts drove major contractions in avian latitudinal distributions throughout the Cenozoic

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Many higher level avian clades are restricted to Earth's lower latitudes, leading to historical biogeographic reconstructions favoring a Gondwanan origin of crown birds and numerous deep subclades. However, several such "tropical-restricted" clades (TRCs) are represented by stem-lineage fossils well outside the ranges of their closest living relatives, often on northern continents. To assess the drivers of these geographic disjunctions, we combined ecological niche modeling, paleoclimate models, and the early Cenozoic fossil record to examine the influence of climatic change on avian geographic distributions over the last ∼56 million years. By modeling the distribution of suitable habitable area through time, we illustrate that most Paleogene fossil-bearing localities would have been suitable for occupancy by extant TRC representatives when their stem-lineage fossils were deposited. Potentially suitable habitat for these TRCs is inferred to have become progressively restricted toward the tropics throughout the Cenozoic, culminating in relatively narrow circumtropical distributions in the present day. Our results are consistent with coarse-scale niche conservatism at the clade level and support a scenario whereby climate change over geological timescales has largely dictated the geographic distributions of many major avian clades. The distinctive modern bias toward high avian diversity at tropical latitudes for most hierarchical taxonomic levels may therefore represent a relatively recent phenomenon, overprinting a complex biogeographic history of dramatic geographic range shifts driven by Earth's changing climate, variable persistence, and intercontinental dispersal. Earth's current climatic trajectory portends a return to a megathermal state, which may dramatically influence the geographic distributions of many range-restricted extant clades.

climate change | niche conservatism | latitudinal diversity gradient | ecological niche modeling | historical biogeography

Extant avian biodiversity is represented by nearly 11,000 living species, which inhabit virtually every conceivable subaerial environment from the poles to the equator (1). However, despite the ubiquity of birds and their penchant for dispersal, extant birdlife is unequally distributed across the Earth. In particular, avian diversity—in terms of both species numbers and higher taxonomic groups—is skewed toward tropical environments on the southern continents (i.e., those that formerly composed the Mesozoic supercontinent of Gondwana).

This pattern led earlier avian historical biogeographic investigations to conclude that vicariance driven by Gondwanan breakup, which was largely completed by the end of the Mesozoic, played a predominant role in triggering deep phylogenetic and geographic divergences within crown birds (e.g., ref. 2). However, recent phylogenetic divergence time studies suggest that most deep divergences within crown birds took place after the Cretaceous–Paleogene (K–Pg) mass extinction (3–7), roughly 66.02 million years ago (8). Although Australia, Antarctica, and South America maintained connectivity into the Paleogene (9, 10), Mesozoic Gondwanan vicariance appears to have played no role in either the diversification or geographic expansion of the avian crown group. Nonetheless, analytical reconstructions of higher order avian historical biogeography invariably recover strong evidence for an origin of most modern diversity on southern landmasses (2, 6, 11).

The crown bird fossil record has unique potential to reveal where different groups of birds were formerly distributed in deep time. Fossil evidence, for example, has long indicated that total-group representatives of clades restricted to relatively narrow geographic regions today were formerly found in different parts of the world (12–23). In particular, the Paleogene record of fossil birds has yielded abundant evidence that many extant clades restricted to southern landmasses had fossil stem-group representatives in the Northern Hemisphere (e.g., refs. 11–13, 15, 19, 21, and 24–38). Collectively, such biogeographic disjunctions between early stem-group representatives and extant taxa cloud our ability to infer ancestral ranges for the deepest crown bird subclades. The general sparseness and Northern Hemisphere bias of the avian fossil record, however, has limited attempts to incorporate bird fossils into large-scale hypotheses of avian biogeographic evolution. Even studies that have integrated phylogenetically constrained avian fossils into analytical reconstructions of ancestral biogeography (6) have been criticized for effectively "swamping out" information from the fossil record by virtue of the limited amount of fossil data compared with extant data in such analyses (39). Thus, ancestral biogeographic reconstructions may have limited potential to reveal whether modern geographic distributions of avian higher clades are truly reflective of their areas of

Significance

The fossil record reveals evidence of dramatic distributional shifts through time for many groups of organisms. One striking example is the early fossil record of modern birds, which shows that many bird groups currently restricted to the tropics were formerly found at high latitudes in North America and Europe. Tracking potentially suitable habitat for these clades over the last 56 million years reveals that cooling trends throughout this period may have largely dictated the geographic distributions of these "tropical" groups, complicating our understanding of where on Earth many of these lineages originated.

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origin or, instead, obscure a history of profound biogeographic shifts throughout their evolutionary history.

The avian fossil record reveals information on where early representatives of various lineages were found and, just as importantly, when in Earth history these birds lived. Paleontological evidence for major fluctuations in avian historical biogeographic patterns therefore raises questions about the extent to which historical factors, such as Cenozoic climatic change, may have been responsible for driving historical shifts in avian geographic range, as has been demonstrated for ectothermic clades, such as turtles (40), and dismissed as a factor influencing the demise of nonavian dinosaurs in the Late Cretaceous (41). Here, we integrate both past and present avian distributional data and climate characterizations to model how habitable regions for 10 neornithine higher level clades (Fig. 1) have changed throughout the Cenozoic. We test whether we can predict the presence of high-latitude Paleogene fossil occurrences of these 10 clades, which are currently restricted to tropical and subtropical latitudes, assuming climatic niche conservatism and given estimates of paleoclimate. On the basis of our analyses, we suggest that climatic changes have played a major role in forcing range contractions for all of these major "tropical" clades toward their present-day geographic distributions. Our results have important implications for the study of avian historical biogeography in deep time and that of other vagile, climatically sensitive clades.

Results

We modeled suitable habitat for 10 neornithine higher level clades using Maxent (42). The number of environmentally unique occurrences used in model calibration ranged from 103 (Leptosomidae) to 9,545 (Trogonidae) (*SI Appendix*, Table S1). Model verification exercises suggest that Maxent models of clade tolerances were statistically significant (P value < 0.05) (*SI Appendix*, Table S1). The discriminatory capacity of the model was evaluated using area under the curve scores; all scores were high and ranged from 0.73 (Trogonidae) to 0.97 (Leptosomidae and Steatornithidae; *SI Appendix*, Table S1).

Suitable conditions were modeled for each clade in the present; these models were then transferred (projected) onto estimates of past climate for four Paleogene time periods with avian fossil records: Ypresian (~56 to 47.8 Ma), Priabonian (~38 to 33.9 Ma), Rupelian (~33.9 to 28.1 Ma), and Chattian (~28.1 to 23.03 Ma) (*SI Appendix*, Figs. S1–S20). We then evaluated whether these paleo-projections correctly predicted penecontemporaneous fossil occurrences for each total clade (Fig. 2 and *SI Appendix*, Figs. S21–S30). Of 19 Paleogene clade/locality occurrences investigated, only 4 were not predicted as highly suitable by our ecological models (Fig. 2 and *SI Appendix*, Figs. S21–S30 and Table S2). Virtually all Ypresian-aged fossil localities were predicted as suitable, but more recent (Priabonian to Chattian) fossil occurrences were predicted with less fidelity (*SI Appendix*, Table S2). Even so, all younger fossil occurrences aside from one (Todidae) were predicted as suitable under at least one paleo-plate and threshold model, and, when suitable habitat was not predicted by our ecological models, it was usually (~60%) found within only 150 km of a clade-specific Paleogene fossil locality—potentially within levels of paleo-plate reconstruction uncertainty (*SI Appendix*, Table S2).

Our ability to predict fossil occurrences was not dependent on the geographic extent of estimated suitable habitat for a given time slice and clade. That is, predicted suitable habitat ranged from only 3.75% [Todidae, maximizing the sum of sensitivity and specificity (MaxSSS) threshold] to 23.61% [Podargidae, least training presence (LTP) threshold] of terrestrial areas globally in fossil-bearing time periods (*SI Appendix*, Table S2). We did not predict suitable conditions for any of these clades at fossil localities in the present day, with the exception of two of the five Coliidae localities (Messel and Walton-on-the-Naze). The relatively broad climatic tolerances of Coliidae may help explain their comparatively late persistence into the Miocene of Europe (22), suggesting that they may have been less susceptible to climate-driven range contraction than the other clades examined (43).

Ecological models were significantly better at predicting fossil occurrences than random expectations based on binomial tests ($P < 0.05$), regardless of threshold or paleo-plate model choice, except for Leptosomidae (significant at $\alpha = 0.096$ for LTP threshold, and $\alpha = 0.078$ for MaxSSS threshold) and Todidae, for which models failed to predict fossil occurrences. Estimates of suitable habitat were more restricted when using the MaxSSS

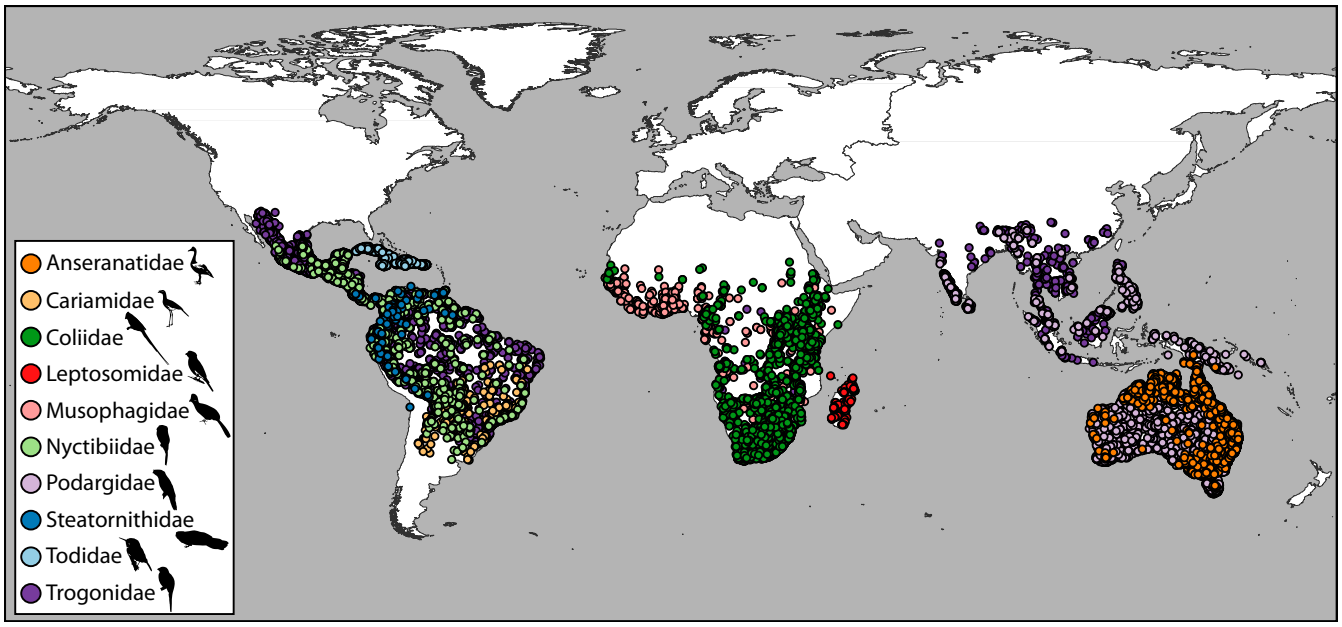

Fig. 1. Present-day occurrences for the 10 neornithine clades studied. Geographic ranges are circumtropical and predominantly restricted to vestiges of Gondwana (Africa, South America, and Australasia).

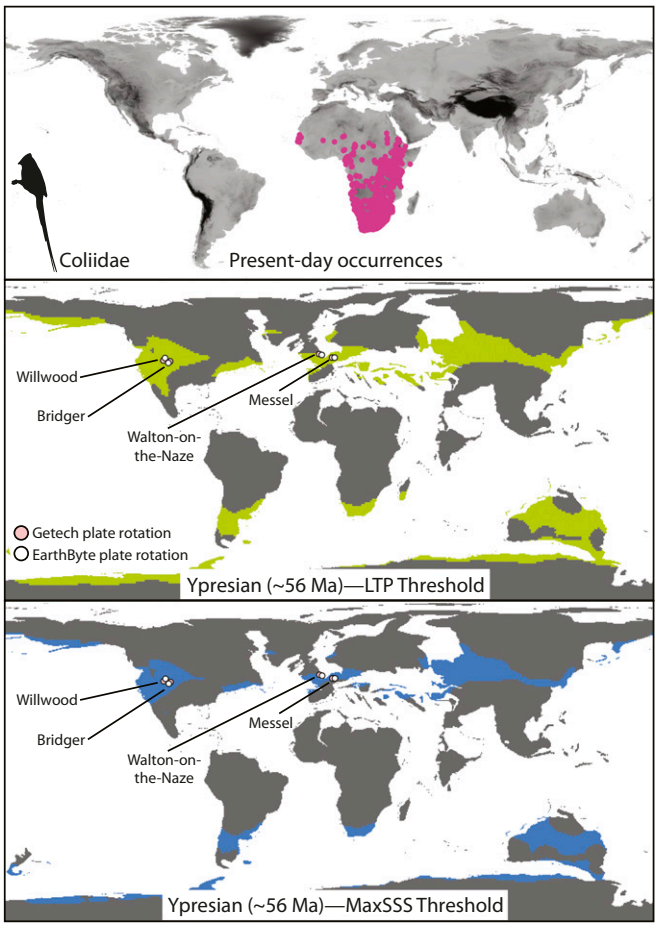

Fig. 2. Present-day occurrences (*Top*) for Coliidae as derived from GBIF. Using these occurrences, models of abiotic tolerances for this clade were projected onto estimates of past climate conditions at the Ypresian, an interval when numerous fossil representatives of this group were deposited. Note the accurate correspondence between fossil localities (shown on map) and model predictions. Maps are shown for both the least training presence (LTP; green) (*Middle*) and MaxSSS (blue) (*Bottom*) threshold methods; pink and white occurrences represent Getech and EarthByte paleo-plate rotational models, respectively (see *Methods* for details). For other clades, see *SI Appendix*, Figs. S21–S30.

threshold (versus LTP threshold), resulting in fewer predicted occurrences for this threshold method (*SI Appendix*, Table S2). The restricted geographic distributions predicted for Leptosomidae and Todidae in the Paleogene are likely a result of their especially narrow present-day distributions, which may complicate ecological modeling (44): Leptosomidae are found only in Madagascar, Mayotte, and the neighboring Comoro Islands while Todidae are endemic to the Greater Antilles and small adjacent islands (45).

Novel environmental combinations can be encountered when projecting ecological models to different regions and/or time periods (46). In these instances, it is difficult to determine, using correlative approaches, whether these unique climatic conditions would be suitable for occupancy by species and higher clades. Although areas predicted as suitable in our paleo-projections were unaffected by novel climate combinations, novel climates were estimated at low latitudes (from approximately ±23° latitude) from the Ypresian to the Chattian. These novel combinations derived primarily from warmer minimum and maximum monthly temperatures estimated for the Paleogene than exist today. Therefore, whether tropical latitudes would have been suitable for these clades in deep time, especially given estimates of extreme Eocene warmth, remains an open question (47). Discoveries of Paleogene fossil birds from low latitudes will be of major importance for clarifying the composition of tropical avian communities in deep time (12).

Most suitable area in the Ypresian was inferred at fairly high latitudes (~40° to 50°), with the bulk of suitable habitat shifting equatorward in a stepwise manner toward the present (Fig. 3). This pattern is evident across all examined clades, with the sharpest contractions of habitable distributions coinciding with the Eocene–Oligocene transition (48, 49), and the next sharpest occurring in the Neogene (Fig. 3 and *SI Appendix*, Fig. S31). As a result, the latitudinal centroid of estimated suitable habitat for each clade moved equatorward through time (Fig. 3 and *SI Appendix*, Fig. S31).

Discussion

Models of suitable conditions for neornithine clades calibrated using modern-day distributional and climate data were able to accurately predict the distributions of these clades' fossil stem-group representatives through the Paleogene, a critical interval in avian evolutionary history, during which many of the deepest neornithine phylogenetic divergences are inferred to have taken place (4–6). This predictive ability was not predicated on broad estimates of the paleo-distributions for studied clades, but rather on narrow bands of suitable habitat estimated at latitudes higher than those occupied by these clades today. Indeed, across our 10 focal clades, we recovered an average difference of ~20° latitude between centroids of suitable habitat predicted for the Eocene (Ypresian) and those predicted for the present day (Fig. 3 and *SI Appendix*, Fig. S31).

The importance of our results is twofold. First, our methods assumed that niche models conditioned on the modern geographic distributions of avian clades accurately encompassed the climatic tolerances of their early stem-group representatives. Although an important source of uncertainty, evidence supporting conservation of clade tolerances over evolutionary timescales has been reported in a variety of clades (50–59). It is striking that we were able to use present-day models of clade tolerances to accurately predict paleo-distributions for these clades' stem-group relatives under conditions estimated to have occurred up to ~56 million years ago, especially in light of the varied ecological habits and geographic distributions of the clades studied (Fig. 2). As such, our results provide first-order support for conservatism of the coarse-scale manifestations of species temperature and precipitation tolerances over geological timescales.

Second, we corroborate climate as a major long-term driver of crown neornithine biogeographic patterns (43, 60). Niche models calibrated on extant clade-level data and projected onto Ypresian to Chattian paleoclimatic reconstructions predicted shifts through time in the centroid of estimated habitable areas of more than 20° latitude for all examined clades. These analyses suggest that Cenozoic climatic change may have been predominantly responsible for driving dramatic shifts in the geographic distributions of these avian clades.

Both Cenozoic paleobiogeography (11, 12, 14, 19, 39, 61) and the timing of the extant neornithine radiation (4–7) cast doubt on Mesozoic Gondwanan vicariance as the mechanism underlying the extreme modern asymmetry of endemic higher order neornithine diversity in the Southern and Northern Hemispheres, raising questions about the origin of pervasive trans-Antarctic avian distributional patterns (2, 62).

A detailed stratigraphic analysis of the European fossil bird record suggests that the assembly of modern avian biogeographic distributions biased toward equatorial latitudes may be the product of two independent waves of geographic range contraction by avian clades throughout the Cenozoic (43). That study noted that a comparatively recent Miocene wave of European

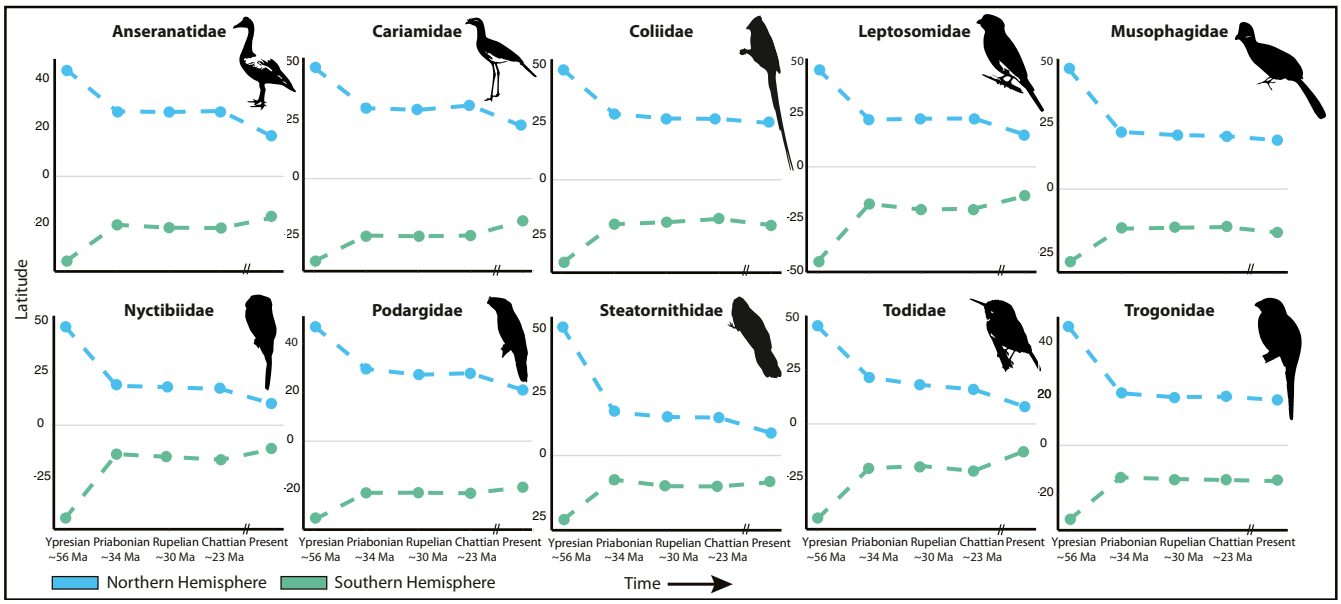

Fig. 3. Temporal shifts in the centroid of suitable habitat for each clade. Binary suitability maps were converted to polygons and used to find the "center of mass" for areas presenting suitable conditions in each time slice; Northern (blue) and Southern (green) Hemispheres were calculated separately. Results are shown for the least training presence (LTP) threshold; see *SI Appendix*, Fig. S31 for MaxSSS threshold results.

extinctions seems to have overwhelmingly affected representatives of clades that are now found in the modern Afrotropical zoogeographic zone [e.g., mousebirds (Coliiformes)] or which currently exhibit pantropical distributions [e.g., parrots (Psittaciformes) and trogons (Trogoniformes)]. In contrast, earlier Paleogene extinctions seem to have eliminated taxa whose crown-group representatives are now found in the neotropics, Madagascar, and Australasia (43). Mayr (12, 43) argued that extirpation of "tropical" European taxa during the Paleogene cannot be attributed reliably to climatic cooling during this period (contra ref. 63) since many "tropical" taxa persisted into the cooler Oligocene and even into the early Neogene. However, the extirpation of "tropical" neornithine taxa in the Paleogene of North America (e.g., ref. 11) may be more reliably attributed to ecosystem changes related to cooling throughout the Eocene (43). Our inferred patterns of long-term contraction of habitable distributions throughout the Neogene (Fig. 3) are consistent with further Miocene climatic cooling driving extirpations and equatorward range contractions (43).

"Paratropical" forests indicative of well-watered, warmer, and more equable climates, such as those persisting at lower latitudes today (64–66), were widespread across North America during the Eocene and coincided with the presence of stem taxa whose crown group representatives are now restricted to lower latitudes. The distribution of these megathermal climates (sensu ref. 67) and associated forests in North America declined substantially toward the end of the Eocene, which had a profound effect on the diversity and composition of North American mammalian and squamate communities (68–72). If many taxa comprising the Paleogene North American avifauna were adapted to megathermal conditions, the extirpation of these taxa from North America may reflect the elimination of these warmer habitats at higher latitudes, resulting in a sharpening of the latitudinal biodiversity gradient (56, 73). Under a model of phylogenetic niche conservatism, habitat tracking may result in broad-scale range constriction, across multiple clades, in response to climate change (71). Indeed, investigations of early Eocene squamate faunas from North America suggest that taxa once common at midlatitudes may have contributed substantially to populating lower latitude biotas in the present day (71). The neornithine fossil record from North America during this interval appears to corroborate this pattern, emphasizing the critical relevance of paleontological data to our understanding of the historical biogeography of extant clades (e.g., refs. 60 and 74).

Estimating the areas of origin of major extant bird clades has emerged as an especially controversial topic in contemporary bird systematics (e.g., refs. 39 and 75), despite ever-improving historical biogeographic models (e.g., refs. 76 and 77) and large-scale avian molecular phylogenies (4–6, 78, 79). We suggest that a primary focus on inferring deep-time areas of origin for major bird clades, which may not be unambiguously discernible given our present knowledge of the avian fossil record (11, 71), overlooks a more achievable goal: discerning the mechanisms that have driven avian range evolution throughout the Cenozoic. This would result in a clearer picture of how and when major avian subclades are likely to have acquired their present-day distributions. We provide quantitative evidence that protracted environmental change throughout the Cenozoic has forced the long-term, equatorward contraction of avian geographic distributions. Delineating between competing biogeographic models whereby major extant clades presently restricted to the tropics originated at low latitudes, or simply became restricted to these areas over the course of the Cenozoic, will rely on renewed focus on Cenozoic fossil avifaunas from Gondwanan continents (12, 75, 80, 81). However, such work has already recovered evidence of extant lineages with restricted distributions, such as total-clade Opisthocomiformes (represented today only by the Amazonian endemic *Opisthocomus hoazin*) occurring on additional Gondwanan and Laurasian continents throughout the Neogene (82, 83).

Although the early Cenozoic avian fossil record is rich (e.g., ref. 12), important temporal and geographical gaps remain. Considering our evidence for apparent avian niche conservatism and habitat tracking over geological timescales, we suggest that the application of ecological modeling tools may provide a first approximation of regions likely to have been inhabited by various bird groups through time, which may aid in guiding paleontological exploration.

Predicting the influence of human-induced climatic change on short- and long-term organismal distributions is an urgent goal in contemporary biology, and projections of major geographic range shifts in the face of Earth's current climatic trajectory are

becoming ever more common (e.g., refs. 84–86). As arguably the most vagile of the major groups of living vertebrates, birds may be more likely than others to undergo dramatic saltational shifts in their geographic distributions, evidenced by historical transoceanic colonization of new continents by extant bird species within historical memory (e.g., refs. 87 and 88). Marginalized across geographic timescales, the frequency of such stochastic dispersal events may explain the apparent habitat-tracking success of birds through the Cenozoic, provided that newly colonized areas are suitable for long-term occupancy by the pioneering species.

While explicit predictions are beyond the scope of the present work, our conclusions would seem to suggest that climatic changes over the coming decades and centuries may induce major distributional changes across the avian tree of life, as has been suggested recently for corals in the marine realm (86). The extremely rapid pace of anthropogenic climate change, however, may instead make it more likely that major groups with restricted distributions are driven to extinction in situ. Unraveling the relative likelihood of these outcomes will be an important goal of future work in avian biogeography and macroecology.

Methods

Full details of our methods are presented in *SI Appendix*, including details of clade selection and model caveats. Supporting data, including environmental layers used to calibrate present-day ecological niche models and median ecological niche models generated from Maxent, are archived open access at Zenodo (89).

Ecological Model Inputs. Distributional data for each extant species within our focal clades were drawn from the Global Biodiversity Information Facility (www.gbif.org) (Fig. 1 and *SI Appendix*, Figs. S21–S30). To characterize present-day climatic landscapes for ecological modeling, we used four environmental variables at 5′ spatial resolution from the WorldClim bioclimatic dataset (90): maximum temperature of warmest month, minimum temperature of coldest month, precipitation of the wettest month, and precipitation of the driest month. Estimates of past climates were simulated for four time periods: Ypresian (~56 to 47.8 Ma), Priabonian (~37.8 to 33.9 Ma), Rupelian (~33.9 to 28.1 Ma), and Chattian (~28.1 to 23.03 Ma). Data were derived from Paleogene simulations produced by two general circulation models (GCMs): FAMOUS (91) and HadCM3L (92, 93).

Ecological Modeling. Clade tolerances were quantified using Maxent v.3.3.3k, a maximum entropy algorithm that estimates suitable environmental combinations for species under a null expectation that suitability is proportional to availability (42). We used present-day environmental conditions to constrain clade tolerances, and resulting models were then projected onto Eocene and Oligocene climatic conditions to estimate the geographic regions that would have been suitable for these clades from the Ypresian through the Chattian. Resulting ecological models produced estimates of suitable abiotic conditions for clades based on present-day climatic characterizations, without consideration of dispersal or biotic constraints.

Postmodeling Analyses. We assessed the ability of paleo-projections of suitable habitat to correctly predict fossil occurrence localities. The correspondence between fossil sites and paleo-projections was analyzed as follows: Fossil sites were transformed (paleo-rotated) so that they reflected their geographical position during the period in which they were deposited. Two paleo-plate models were used for transformations: Getech (93) and EarthByte via the PaleoGIS extension for ArcGIS (94). Localities were accorded a buffer of 25 km using the "gBuffer" function in the "rgeos" package for *R* (95). Localities were buffered to account for uncertainty in both paleo-plate rotations and georeferencing and to reflect the minimum likely area the fossil would have occupied when extant. These buffered localities were then intersected with the suitable area predicted for the time period corresponding to the age of the fossil site, using a custom script written in *R*.

We assessed the probability of randomly predicting fossil occurrences for each clade in each time slice using binomial tests (96). Analyses were performed for each clade characterized by more than one occurrence in a given time slice, using the following parameters: n = the number of successfully predicted occurrences, K = the total number of occurrences, and P = the probability of successfully predicting an occurrence, defined by the percentage of predicted suitable terrestrial area globally.

Temporal shifts in the centroid of suitable habitat predicted for each clade were calculated using the "gCentroid" function in the "rgeos" package for *R* (95). The binary suitability maps were converted to polygons, and these polygons were used to find the "center of mass" (also known as "true centroid") of the areas presenting suitable conditions for each time slice; Northern and Southern Hemispheres were calculated separately (Fig. 3 and *SI Appendix*, Fig. S31).

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